



Untangling the imprints of climate, geography and land use/cover on bird diversity in the South American Gran Chaco

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Abstract

Aim: To evaluate the structure of bird communities throughout the South American Gran Chaco determining the effects of climate, geography and land use/land cover in bird beta diversity, as well as to understand the beta diversity processes underlying land use changes across broad spatial ranges.

Location: South American Gran Chaco.

Taxon: Birds.

Methods: We constructed a site-by-species matrix with occurrence probabilities of 293 bird species across 2,669 spatial units tiling completely the study area. Based on this matrix, we calculated pairwise dissimilarities scores and performed a hierarchical cluster analysis for describing the spatial configuration of dissimilarities. The clustering result was spatially represented through an original venation map with boundaries between sites widened in the function of their distance in the dendrogram. We used the Generalized Dissimilarity Modelling approach to model beta diversity, using geographic distance, climatic and land use/land cover information as predictors. We mapped beta diversity patterns using colour theory and the HSV colour model.

Results: We identified two main clusters of sites across the Gran Chaco, which represent environmentally different sites and harbour very distinct assemblages of species. These main groups are separated by two natural delimiters: The Bermejo-Pilcomayo interfluvium and the Lower Paraná floodplain. Overall, we observed that the percentage of cropland and climatic variables were important shapers of bird beta diversity.

Main conclusions: We provide the first area-wide assessment of land use/land cover effects on bird beta diversity for the Gran Chaco. The distribution of croplands has a marked influence on bird beta diversity at regional scale highlighting the role of anthropic changes in reshaping bird beta diversity within the ecoregion. Taking into account the global increasing conversion of forests into croplands, a growing footprint of land use changes over geographical patterns of bird diversity in forest biomes can be anticipated.

KEYWORDS

beta diversity, bird communities, dry forest, endangered ecosystems, GDM, land use, species distribution

1 | INTRODUCTION

Land use change is one of the most relevant processes that drive the dynamics of biological diversity (Dormann et al., 2007; Peters et al., 2019). Human activities often generate completely novel landscapes, with unpredictable changes to alpha-, beta- and gamma-diversity (Socolar, Gilroy, Kunin, & Edwards, 2016). Therefore, giving that detailed gamma diversity studies at regional scales are difficult to achieve, Socolar et al. (2016) argued for the need to understand the processes underlying beta diversity patterns and its behaviour under scenarios of land use change. From this perspective, beta diversity represents a key concept for understanding ecosystem functioning and management, complementing the alpha-scale researches and leading to management practices aligned to broad scope for biodiversity conservation (Legendre, Borcard, & Peres-Neto, 2005; Socolar et al., 2016).

The main drivers behind beta diversity differ through spatial scales (e.g. Gaston et al., 2007; Melo, Rangel, & Diniz-Filho, 2009), and their effects may vary according to taxonomic groups (Socolar et al., 2016). For instance, plants and spiders show opposite trends (increasing and decreasing beta diversity respectively) across conventional and organic croplands in Europe, while deforestation has different effects on the soil bacterial beta diversity either reducing or increasing it in the Brazilian Amazon or Borneo respectively (Socolar et al., 2016). At the regional scale, climate and habitat heterogeneity seem to be the main determinants of bird beta diversity (Corbelli et al., 2015; Keil et al., 2012; Veech & Crsit, 2007). More effort is necessary to understand the role of environmental and biotic factors on beta diversity across broad spatial ranges (Antão, McGill, Magurran, Soares, & Dornelas, 2019).

Although knowledge about the effects of land use change on species richness has increased considerably in recent years (Koivula et al., 2017; MacGregor-Fors & Schondube, 2011; Rittenhouse et al., 2012), its effect on beta diversity has been little explored (Barnagaud et al., 2017; Corbelli et al., 2015; Jeliashkov et al., 2016). This asymmetry is still more marked in less-studied regions such as the South American dry forests. These forests have experienced an increasing rate of deforestation, especially in the Brazilian Cerrado, the Chiquitano Forests in Bolivia and the Gran Chaco in Bolivia, Paraguay and Argentina (Baumann et al., 2017). In the last 30 years, the Gran Chaco has become a hotspot of agricultural expansion and intensification, as cattle ranching and agriculture have expanded at the expense of forests (Baumann et al., 2017). The Gran Chaco's bird richness is particularly sensitive to land use changes, declining in a gradient from natural habitats to implanted pastures and croplands (Macchi, Grau, Zelaya, & Marinaro, 2013). Additionally, bird assemblages in natural grasslands show low similarity when compared with those from implanted pastures (Macchi et al., 2013). Thus, while open habitats would be important for biodiversity in the landscape configuration of the Gran Chaco, the novel open habitats created by cattle ranching and agriculture lead to local species extinction (Torres, Gasparri, Blendinger, & Grau, 2014) and high unpaid extinction debt (Semper-Pascual et al., 2018). Land use changes are creating novel

ecosystems that would result in new combinations of bird species and modified relative abundances that differ significantly from other ecosystems in the same region (Morse et al., 2014).

The South American Gran Chaco is characterized by a rich birdlife but with a few endemics. It is compositionally influenced by surrounding biomes with which it has controversial biogeographic relations (Porzecanski & Cracraft, 2005; Prieto-Torres, Rojas-Soto, Santiago-Alarcon, Bonaccorso, & Navarro-Sigüenza, 2019; Short, 1975; Straube & Di Giacomo, 2007). Despite the numerous surveys about deforestation/fragmentation and studies on priority conservation areas in the Chaco dry forest (e.g. Andrade-Díaz, Sarquis, Loiselle, Giraudo, & Díaz-Gómez, 2019; Nori et al., 2016), few studies have assessed the diversity patterns and relationships among the entire avifauna across the whole region. Most of the information collected in Chaco avifaunal studies comes from a small number of areas, so it is risky to formulate generalizations on biota dynamics because of the lack of replication (Straube & Di Giacomo, 2007). Therefore, many questions have yet to be answered regarding the macroecological spatio-temporal patterns of the Chaco avifauna (Herzog y Kessler, 2002; Nores, 1992).

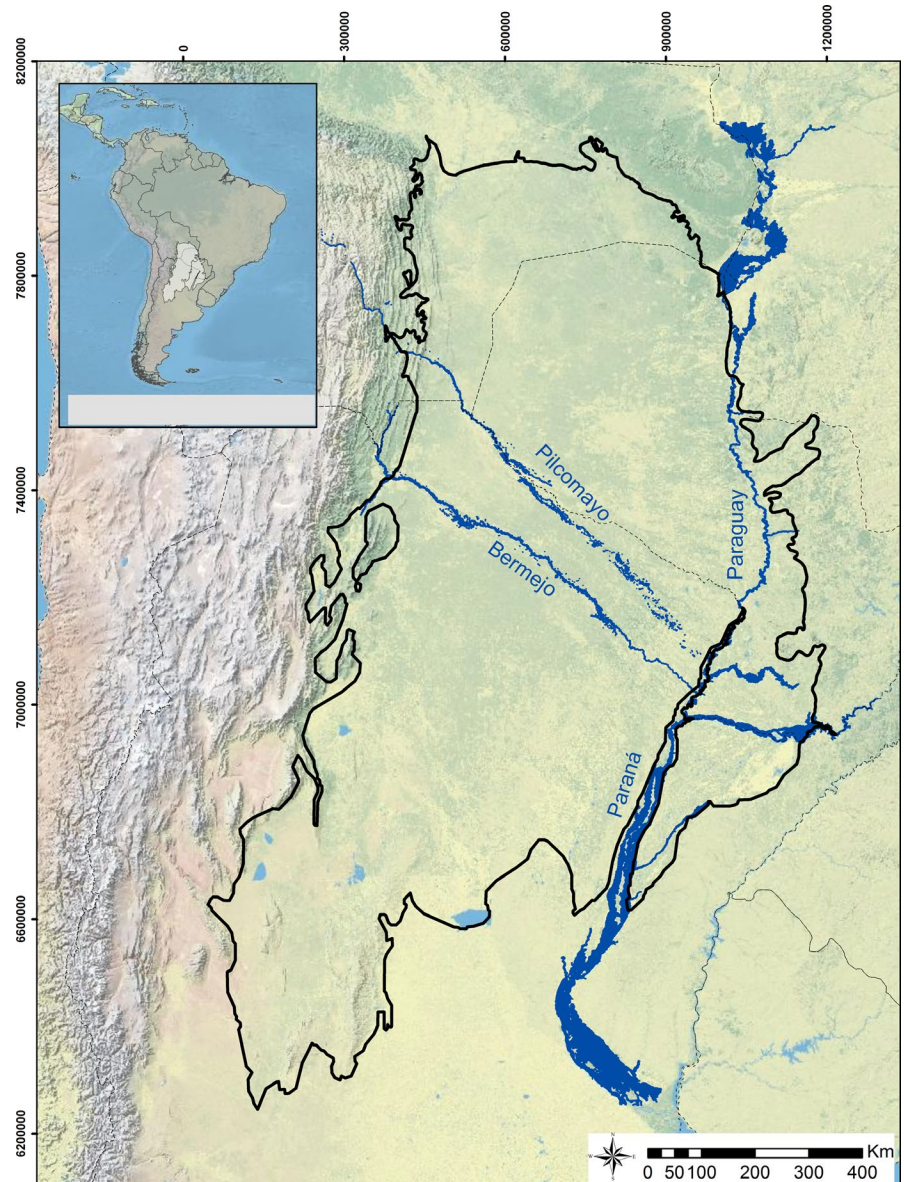
This paper aims to study the bird community structure and composition across the South American Gran Chaco and to untangle the role of different environmental and land use/land cover variables on the bird beta diversity. To achieve these goals, we firstly analysed the spatial configuration of bird species richness and secondly mapped the hierarchical clustering of sites guided by their avifauna dissimilarities. These analyses are on the path to achieve a better understanding of the spatial structure of the Chacoan bird diversity. They are necessary to interpret better the beta diversity patterns to be explored subsequently. Finally, we used Generalized Dissimilarity Modelling (GDM) to analyse the bird beta diversity in the South American Gran Chaco and to recognize both the unique and shared contributions of predictors (climate, geography and land use/land cover information) in explaining the data.

2 | MATERIALS AND METHODS

2.1 | Study area

The South American Gran Chaco (Figure 1) is a vast tropical and subtropical dry forest region that occupies 1.1 million km² over part of Bolivia, Argentina, Paraguay and a small portion of Brazil, comprising the Dry Chaco and the Wet Chaco sub-ecoregions (Olson et al., 2001). Its terrain is mainly flat, except for the west and southwest, where low elevation mountain ranges run. The climate is semi-arid and highly seasonal, with a distinct dry season in autumn and winter (May–September), and a warm, wet season in spring and summer (November–April). The rainfall gradient decreases westwards from 1,200 mm in the Wet Chaco to 450 mm in the Dry Chaco (Bucher, 1982). The mean annual temperature is around 22°C, with an average monthly maximum of 28°C. The vegetation is a mosaic of dry forests, open woodlands, scrublands, savannas and grasslands (Bucher, 1982;

FIGURE 1 Study area: The South American Gran Chaco with its main watercourses



Clark, Aide, Grau, & Riner, 2010). The large extent of the area in addition to the wide variety of environments favour a high diversity of animal and plant species, and therefore, make Chaco a key area for biodiversity conservation (The Nature Conservancy, Fundación Vida Silvestre Argentina, Fundación DesDel Chaco, & Wildlife Conservation Society, 2005).

Short (1975) listed more than 400 breeding bird species in the region, most of them restricted to South America. However, the number of truly endemic species is low (Stotz, Fitzpatrick, Parker III, & Moskovits, 1996). Many bird species occurring in the Gran Chaco are widespread and range far beyond its limits (Short, 1975). Chacoan bird species richness decreases from north to south (Rabinovich & Rapoport, 1975). Surrounding regions like the Andes to the west, the Atlantic Forest to the northeast and the Pampas and Patagonia to the south would influence it (Straube & Di Giacomo, 2007). A comparative historical analysis of robust phylogenies predicted that Chacoan bird species would be more closely related to the Cerrado than to Caatinga species, and less

to other biogeographical areas (Porzecanski & Cracraft, 2005). Besides, numerous wetlands distributed mainly to the east of the Gran Chaco provide suitable habitats for aquatic birds. Large marsh ecosystems are major breeding sites for resident species and receive huge numbers of non-breeding migrants (Stotz et al., 1996).

Historically, much of the region has been severely degraded by extensive cattle ranching and subsistence agriculture in addition to timber and charcoal extraction (Clark et al., 2010). Still, the conversion of forests to agriculture has experienced increasing rates over the past 30 years. In that period, more than 142,000 km² of the Chaco's forests, equalling 20% of all forest, was replaced by croplands (38.9%) or grazing lands (61.1%). The relative forest loss was higher in the wet Chaco (19.8%) than the dry Chaco (18.2%; Baumann, Piquer-Rodríguez, Fehlenberg, Gavier Pizarro, & Kuemmerle, 2016). Forests have been replaced mainly by croplands in Argentina; meanwhile, deforestation followed by pastures has especially taken place in Paraguay. In turn, the Bolivian Chaco was the less modified area (Baumann et al., 2017).

2.2 | Species distributions

2.2.1 | Habitat suitability models

We performed habitat suitability models in MaxEnt v3.3.1 using species presence data from all the Gran Chaco region along with nine environmental variables: annual mean temperature, annual precipitation, distance to water bodies, slope and five land use/land cover classes (henceforth called LULC, concerning with percentages of forest, natural grassland, cropland, pasture and others, the latter mainly being associated with water bodies and human buildings). Data sources are in Appendix 1 while the complete list of presence records by species is available in Appendix S1. To minimize the complexity of models, we used only linear and quadratic features, and we determined the optimal value for the regularization coefficient (β) for each species (Cobos, Peterson, Barve, & Osorio-Olvera, 2019). For each species, we recovered the predicted map of presence from the constructed model (binary output). The choice of species, variables and the modelling process is fully described in Appendix S2. We recognize that models trained with presence data collected only from the Gran Chaco region may have lower performance than models trained with presence data of the full species' ranges (Carretero & Sillero, 2016; Raes, 2012). However, as our goal was to analyse the effect of both environmental and land use variables on bird beta diversity, and given that the land use layers we used were developed specifically for the Gran Chaco, we narrowed our calibration area to that region. In any case, after selection of the species that met all the reliability requirements for further use (Appendix S2), one of the authors (PGB) made a final selection evaluating the fit of the modelled distributions with current knowledge on species' distributions according to his extensive experience in the field and specific literature (e.g. del Hoyo, Elliot, Sargatal, Christie, & Kirwan, 2019; Herzog et al., 2016).

2.2.2 | Site-by-species matrix

The presence/absence maps obtained from the habitat suitability models were rasters in a 3×3 km resolution. To facilitate subsequent calculations, we transformed the original maps to another of coarser resolution (i.e. units of 21×21 km resolution after grouping 7×7 cells). These larger spatial units are called hereafter as sites. Previously, we had verified that clustering obtained with this coarse resolution did not differ from clustering performed at finer resolutions in terms of the optimal number of clusters as well as spatial range of larger and subordinated clusters in their hierarchical assortment. After grouping pixels into sites, the single binary maps resulted in maps with continuous values ranging from 0 (complete absence) to 1 (full presence) accounting for the occurrence degree of species in sites. For each site i , these values can be interpreted as the occurrence probability of a given species within such site i . Mathematically, the resulting distribution map can be encoded into

a site-by-species matrix $\mathbf{R} = [r_{ij}]$ in which each entry r_{ij} denotes the probability of occurrence of species j into site i .

2.3 | Analysis of distributional matrix

Each row of the site-by-species matrix represents the structure of bird assemblage for a given site. Technically, it corresponds to a multivariate binary response. So, summation over all the entries of a row (i.e. probability scores) retrieves the mathematical expectation or average number of species for the respective site.

We calculated dissimilarities between sites using the complement of the Positive Matching Index (i.e. $1 - \text{PMI}$, Dos Santos & Deutsch, 2010). We calculated three parameters (a , b and c) from the matrix \mathbf{R} of occurrence probabilities for species across sites. The parameter a represents the number of common species between sites under comparison; b and c count the species recorded for one of the two sites. As each row of \mathbf{R} can be likened to a multivariate binary variable, the average count of items under random sampling from such variable is obtained as the sum of all probability scores involved (i.e. summation over all entries of a row). Therefore, the required triad of parameters are embodied in their respective symmetric matrices $\mathbf{A} = [a_{ij}]$, $\mathbf{B} = [b_{ij}]$ and $\mathbf{C} = [c_{ij}]$ of inter-site comparison. They can be calculated as follows: $\mathbf{A} = \mathbf{R} \cdot \mathbf{R}^T$, $\mathbf{B} = \mathbf{R} \cdot (\mathbf{1} - \mathbf{R})^T$ and $\mathbf{C} = (\mathbf{1} - \mathbf{R}) \cdot \mathbf{R}^T$. The calculated matrix of compositional dissimilarities between sites is the input for (a) clustering and (b) beta diversity modelling.

Using this dissimilarity matrix, we perform hierarchical clustering (Becker & Chambers & Wilks, 1988). This technique allows us to explore data and look for discontinuities and clear cut segregation of ecological units. Robust clusters consist of a set of sites characterized by high within-group and low between-group similarity. It portrays valuable cues to interpret results coming from beta diversity modelling. For each meaningful cluster, a list of supporting species is provided. Species are considered as diagnosing elements of a cluster whenever their distributions overlap significantly with the set of spatial units comprising such cluster. Statistical significance is assessed by calculating the probability of set intersection (Kalinka, 2013). A low probability score (set here at 0.01) means that the overlap size is large enough to be expected by random chance. Empirically, statistical significance occurs when the similarity between clusters and species spatial distributions, measured through the above-mentioned PMI index, is larger than 0.6.

The identification and posterior mapping of clustering configuration help to recognize the spatial nature of dissimilarity data. Here, we also introduce an innovative way to map the salient features of the clustering obtained. We just focus on the very first three instances of dichotomy across the dendrogram ending up with eight clusters. The intercluster boundary or, technically speaking, the geometrical bisector between two sites from different clusters, is represented in the map through concatenated segments where the line width depends on the level at which the dendrogram is cut for



obtaining clusters. Thus, line width between sites segregated into distinct clusters after the first bipartition of the dendrogram is much wider than that of sites separated from each other at a lower dissimilarity level. The final output allows the reader to recognize the spatial domain of clusters. Due to its similarities with the hierarchical leaf vein system of angiosperms (where the veins of higher branching orders have smaller diameters; Sack & Scoffoni, 2013), we named this map as the *dissimilarity venation map*. We performed all these procedures with the R statistical software (R Core Team, 2018).

2.4 | LULC data analysis and mapping

We performed a compositional data analysis over the LULC profiles of sites. Details are provided in Appendix S3. The LULC layers represent compositional data since scores for each LULC class are proportions of the total coverage and are therefore interdependent (Aitchison, 1982). We explored this data through principal component analysis adjusted to compositions (Aitchison PCA) since this technique accounts for the covariations among parts. We obtained a compositional biplot to see these covariations through the R package *robCompositions* (Templ, Hron & Filzmoser, 2011). We generated an LULC map to assess visually the relative contribution of LULC categories, using for that purpose the HSV (hue, saturation and value) colour model. See Appendix S3 for additional details about the calculation process. This step is critical for a better understanding of the spatial nature of LULC variable.

2.5 | Analysis of beta diversity

2.5.1 | Generalized dissimilarity modelling

We used GDM analysis (Ferrier, Manion, Elith, & Richardson, 2007) to reveal patterns of beta diversity and to predict the compositional dissimilarity between sites across the Gran Chaco. This approach allows to estimate the magnitude and rate of species turnover along environmental/geographical gradients, by considering the dissimilarity between pairs of sites as a function of their environmental difference and geographical distance (Fitzpatrick et al., 2013). We use the R package *gdm* (Manion et al., 2017), selecting the default option of three I-spline basis functions per predictor. The I-spline functions describe the relationship between beta diversity and the gradient and hold information about the contribution of each input variable (Ferrier et al., 2007). We tested overall model significance by using Monte Carlo permutations on the input matrix of predictors followed by calculation of the explained deviance.

To evaluate the importance of LULC classes in influencing beta diversity, we fitted separate I-splines for each of them. The LULC predictors were the respective percentages of Forest, Natural grassland, Cropland, Pasture and Other features (wetlands and human buildings), as in Baumann et al. (2017) with modifications (see

Appendix S2). We included the geographic distance between pairs of sites as a predictor variable to correct the effect of spatial autocorrelation. We used Annual mean temperature and Annual precipitation variables (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) to assess climatic effects.

2.5.2 | Unique and shared effects of predictors

We deal with three sets of predictors, namely the climatic, geographical and LULC variables. Shared and unique contributions in percentages in explaining the deviance of the null model were inferred by computing the explained deviance of all the possible models. We start the calculation with all available predictor variables, deleting one class of variables at a time until we arrive at models based on single predictors. Then, with the aid of overlapping set equations based on 3-set Venn diagram operations, the different contributions were recognized. Percentages were graphically depicted through a sectorized circle of total radius proportional to the total amount of information to be explained (i.e. deviance of null model). The outer ring would correspond to the unknown component, the middle ring is sectorized like a pie chart and accounts for the unique and 2-set shared contributions, and finally, the inner circle is proportional to the 3-set overlap.

2.5.3 | Beta diversity map

To graphically represent dissimilarities between pairs of sites we used the multidimensional scaling applied on the reweighted matrix of dissimilarities (Dos Santos, Cuzzo, Reynaga, & Domínguez, 2011) as implemented by the function *reweight* in the R package *SyNet* (Dos Santos, 2011). This procedure promotes a two-dimensional representation of data points that resembles a circle. The structure of the dissimilarity matrix can thus be represented with data points arranged in the perimeter of a closed two-dimensional shape, ideally a circumference, and can be tied to angular positions and then assigned with colours accordingly. In colour theory, the hue is the characteristic or appearance parameter that defines the pure tone and is represented by angular positions around a central point. Consequently, the colouring of data points proceeds by matching their angular positions with those of hues in the colour wheel.

3 | RESULTS

3.1 | Analysis of distributions

We obtained a distributional matrix of 2,669 sites \times 293 bird species from habitat suitability models (available in Appendix S4). A minor percentage of the modelled species (i.e. 10%) showed ranges spanning >60% of the region, while a huge number of species (i.e. 80%) occupied less than half of the region. Expected richness was

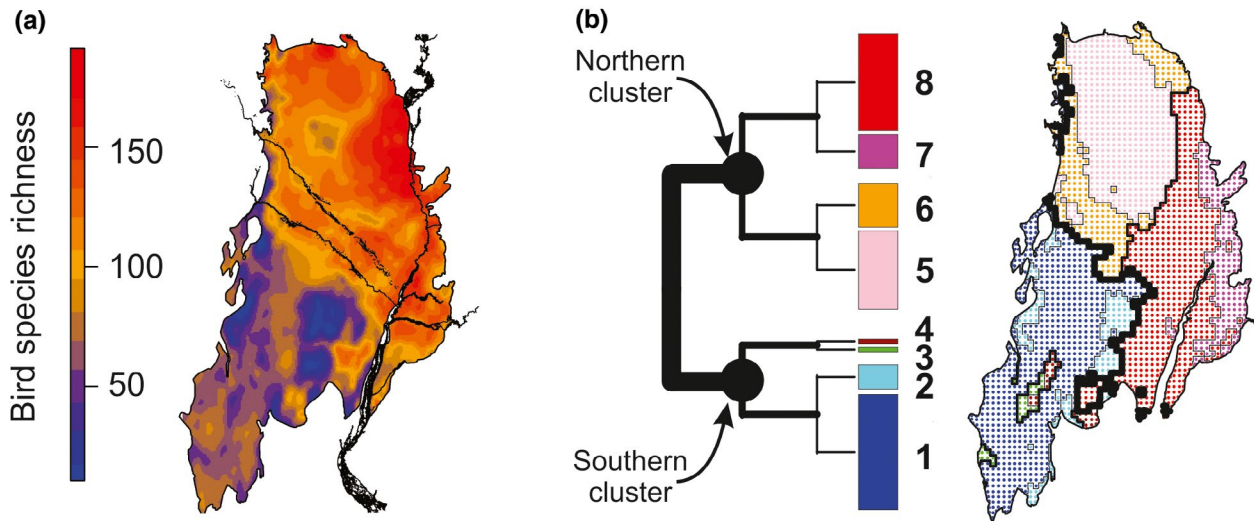


FIGURE 2 (a) Expected bird richness. The main rivers of the Paraná drainage network have been projected onto the map. (b) Dissimilarity venation map. To the left, hierarchical grouping of sites based on their dissimilarities. The cluster configuration is shown up to the third divisive level of the respective dendrogram. Size of rectangles at the tips proportional to the area of the cluster. To the right, spatial expression of clusters already identified. The boundaries are widened depending on the dissimilarity between clusters to which adjacent sites belong to

not homogeneously distributed, with maximum values (c. 192 species) in the northeast of the region and decreasing to the southwest (Figure 2a). The decline in richness was particularly marked to the south of the Pilcomayo-Bermejo interfluvium, dropping until ten species in certain areas. Interestingly, these poorest sites were aggregated into spatially disjoint sets.

The hierarchical clustering of sites resulted in two main clusters on both sides of rivers Bermejo and Lower Paraná (hereafter Northern and Southern clusters; Figure 2b). Figure 2b also shows through the dissimilarity venation map the assortment of sites within subsequent clusters. The Northern cluster occupied the largest part of the region, approximately two-thirds of it, while the Southern cluster occupied only one-third (Table 1). Contiguity in space is more common for the sub-clusters found at the Northern portion than those of the Southern counterpart, which is patchier in this regard. On average, species richness in the Northern cluster is twice as much as in the Southern cluster, and it represents 40% of the total number of species under consideration (Table 1).

3.2 | LULC data analysis

The first two components of the covariance biplot explained 76% of the variance in the data (Figure S3 1). Forest exhibited a higher variation relative to all LULC classes across data points. The link between the tips of the rays of Cropland and Forest passes through the tip of the ray of Pasture. This indicates that these three categories are linearly related. In this case, when Forest increases, the other two will decrease. Additional details about the interpretation of biplot are provided in Appendix S3.

As a whole, Forest expanded over 56% of the region, Pasture and Cropland over 25%, Others occupied around 15% and Natural grasslands were less represented. Forested sites surrounded the

main nucleus of pastures at the Northern cluster of sites in Paraguay (Figure 3). At the Southern cluster, croplands developed at two separate bands separated by forested sites. Thus, productive areas were more patchily distributed to the south than to the north of Gran Chaco. Croplands and Pastures were intermingled with natural grasslands to the south and east of Chaco (Figure 3).

3.3 | Analysis of beta diversity

The model fitted the data significantly and explained 79.87% of the deviance (Table 2, Figure 4a). The shape of the fitted I-splines for variables associated with beta diversity was nonlinear, suggesting a complex behaviour for the compositional turnover rate along the gradient (Figure 4b–e). Most predictors reached a plateau after a given threshold, although a few variables (notably %Cropland) behaved non-asymptotically.

Taking into account the magnitude of effects (maximum height achieved by I-splines), %Cropland, Annual precipitation and Annual mean temperature were the dominant variables (Table 2). Climatic variables are geographically structured, so they share a large percentage in explaining the model deviance, but they remain little associated with LULC variables (Table 2, Figure 4f). The upper concavity of the %Cropland curve means that the turnover came slowly in sites with scarce crops, but increased as the percentage of crops increased. Contrarily, the lower concavity of Annual precipitation and Annual mean temperature means that compositional dissimilarity increased quickly at relatively lower values of both variables, but more slowly beyond 1,000 mm and 24°C respectively.

We compressed the information about compositional dissimilarities into a 2D spatial representation of data (Figure 5). The resulting map of beta diversity is displayed in Figure 5e. Chromatic contrasts observed in the map parallel those already observed in Figure 2b

TABLE 1 Main characteristics of clusters defined through Figure 2b. Numbering of elemental clusters identical to those of such figure. The overall area covers 1,078,101 km². For a given set of elemental clusters, <S> represents the average species richness to be recorded in there, and |S_{>50%}| indicates the total number of species that have more than half of their expected distributions embedded within the respective cluster. Species are included in the list of supporting or diagnosing entities whenever the overlap between their spatial ranges and the area of clusters are large enough to yield a significant similarity measure, namely a PMI score over 0.6

Lower level of clustering								
Clustering	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}
% Area	28.62%	6.07%	1.12%	1.12%	19.60%	10.94%	8.47%	24.05%
< S >	65	27	48	65	122	114	130	115
S _{>50%}	49	0	0	0	18	2	12	56
Diagnosing species	Cyanoliseus patagonus, Hirundinea ferruginea, Leptasthenura platensis, Pseudoseisura lophotes, Rhynchospiza strigiceps, Sappho sparganurus, Spizapteryx circumcincta				Crypturellus undulatus, Micrastur semitorquatus, Nothura boraquira, Synallaxis albilora		Alectrurus risora, Anthus nattereri, Dacnis cayana, Elaenia flavogaster, Forpus xanthopterygius, Gubernetes chihui yetapa, Pseudoisestes guirahuro, Sporophila bouvreuil, Sporophila leucoptera, Turdus leucomelas	Dendroceryna viduata, Platalea ajajia, Plegadis chihui
Intermediate level of clustering								
Clustering	{1, 2}	{3, 4}	{5, 6}	{7, 8}				
% Area	34.69%	2.25%	30.54%	32.52%				
< S >	58	57	119	119				
S _{>50%}	50	0	75	108				
Diagnosing species	Nothura darwini, Serpophaga munda, Turdus chiguaco		Amazona aestiva, Campephilus melanoleucos, Campylorhamphus trochilostrius, Cantorchilus guarayanus, Chaetura meridionalis, Claravis pretiosa, Coccyzus americanus, Columba squammata, Crypturellus parvirostris, Falco ruficularis, Formicivora melanogaster, Geranospiza caerulescens, Herpetotheses cassinans, Icterus croconotus, Ictinia plumbea, Inezia inornata, Myiothlypis flaveola, Myrmorchilus strigilatus, Patagioenas cayennensis, Phacelodromus ruffifrons, Phaeomyias murina, Primolius auricollis, Sarcoramphus papa, Sarkidiornis melanotos, Sporophila lineola, Thamnophilus sticturus	Agelasticus cyanopus, Amazonetta brasiliensis, Amblyramphus holosericeus, Anthus lutescens, Anumbius anumbi, Aramides ypacaha, Aramus guarauna, Arremon flavirostris, Arundinicola leucocephala, Basileuterus culicivorus, Butorides striata, Cacicus haemorrhous, Calidris melanotos, Certhiaxis cinnamomeus, Ciconia maguari, Circus buffoni, Colaptes campestris, Conirostrum speciosum, Dendrocolaptes platyrostris, Donacobius atricapilla, Emberizoides herbicola, Emberizoides ypiranganus, Gallinago paraguayae, Hirundo rustica, Ixobrychus exilis, Megarynchus pitangua, Myiarchus ferox, Nothura maculosa, Pachyrhamphus validus, Paroaria capitata, Phacelodomus ruber, Phalacrocorax brasiliensis, Phimosus infuscatus, Porphyrio martinicus, Porzana albicollis, Progne chalybea, Pseudocolaptes flavigentris, Pseudocolaptes sclateri, Rhynchotus rufescens, Rosthamus sociabilis, Satrappa icterophrys, Sporophila collaris, Sporophila hypoxantha, Sporophila ruficollis, Sturnella superciliosa, Tachycineta leucorhoa, Thylopsops sordida, Trogon surrucura, Veniliornis passerinus, Xolmis cinereus				

(Continues)



TABLE 1 (Continued)

Higher level of clustering	
Clustering	{1, 2, 3, 4}
% Area	36.94%
< S>	58
S _{>50%}	52
Diagnosing species	Knipolegus aterrimus, Sturnella loyca
	Anhinga anhinga, Aratinga nenday, Ardea cocoi, Bartramia longicauda, Busarellus nigricollis, Buteogallus meridionalis, Buteogallus urubitinga, Cacicus chrysopterus, Cacicus solitarius, Cairina moschata, Campylorhynchus turdinus, Casinornis rufus, Cathartes burrovianus, Celeus lugubris, Charadrius collaris, Chauna torquata, Chordeiles nacunda, Chrysomus ruficapillus, Cnemocticus fuscatus, Columbiga talpacoti, Crotophaga ani, Crotophaga major, Dendrocycyna autumnalis, Dolichonyx oryzivorus, Dryocopus lineatus, Elaenia spectabilis, Fluvicola albiventer, Gnorimopsar chopi, Hylocharis chrysur, Icterus pyrrhopterus, Jabiru mycteria, Jacana jacana, Machetornis rixosa, Melanerpes candidus, Milvago chimachima, Mycteria americana, Myiarchus tyrannulus, Nyctibius griseus, Nyctidromus albigollis, Pachyrhamphus viridis, Paroaria coronata, Playa cayana, Piculus chrysochloros, Pionus maximiliani, Psittacara leucophthalmus, Pyrocephalus rubinus, Ramphastos toco, Rhea americana, Riparia riparia, Rynchops niger, Saltator similis, Schoeniophylax phryganophilus, Stegidopteryx ruficollis, Tachybaptus dominicus, Tachyphonus rufus, Tapera naevia, Thamnophilus doliatus, Theristicus caerulescens, Thraupis sayaca, Tigrisoma lineatum, Tolmomyias sulphurescens, Tringa solitaria, Volatinia jacarina

and match natural dividers such as the Bermejo-Pilcomayo interfluvium and Lower Paraná influence area. The distinction between the Northern and Southern clusters of sites is clearly detectable in the 2D scatter after multidimensional scaling (Figure 5d) and is also easily perceived on the map. The Northern portion is longitudinally striped, whereas the Southern counterpart shows a more convoluted aspect for the sites identically coloured (and so, more similar between them in bird composition).

4 | DISCUSSION

In this paper, we provide the first area-wide assessment of LULC effects on the beta diversity of birds for the whole Gran Chaco. The area is currently under several anthropization processes (Baumann et al., 2017), and we show that cropland is the major LULC class in explaining the beta diversity patterns at the regional scale. We also analysed the structure of bird communities and their spatial patterns of diversity inside the Gran Chaco. We show that the distribution of bird richness is higher, and bird communities are compositionally more different in the northern than in the southern part of the Gran Chaco. These sub-regions are mainly defined by latitude rather than the traditional longitudinal subdivision of the Gran Chaco largely based on precipitation gradient and floristic composition: western Dry Chaco versus eastern Wet Chaco (Bucher, 1982). LULC exhibited a great impact on the spatial distribution of the avifauna with a unique effect as relevant as the combined effects of geographic distance and climate. When considering all variables individually, croplands outweigh the remaining ones. Thus, anthropogenic landscape changes can be reshaping bird beta diversity within the Gran Chaco. This is especially important for management policies since tropical and subtropical dry areas are experiencing an accelerated rate of land use change.

4.1 | The two faces of the Chacoan avifauna

This is the first study that explores the patterns of bird diversity on a regional scale for the South American Gran Chaco in the last 40 years, and the first that attempts to understand how different environmental variables (natural and anthropogenic) may influence them. Almost 50% of the Chaco avifauna was reported by Short (1975) as widely distributed across the region. Our results, in contrast, showed that most Chacoan bird species have an intermediate to narrow rather than wide range size within the Gran Chaco and that almost 80% of the species occupy a total area less than half of the entire region. To a large extent, these differences are explained by the greater precision of distribution maps obtained with niche modelling compared with the information available four decades ago.

As reported for many taxa in the Neotropics (e.g. Hawkins, Diniz-Filho, Jaramillo, & Soeller, 2006; Rull, 2011), we found herein a negative relationship between the latitude and richness. The Chacoan avifauna is firstly divided into two large dissimilar clusters of communities at both sides of a divider running along the direction

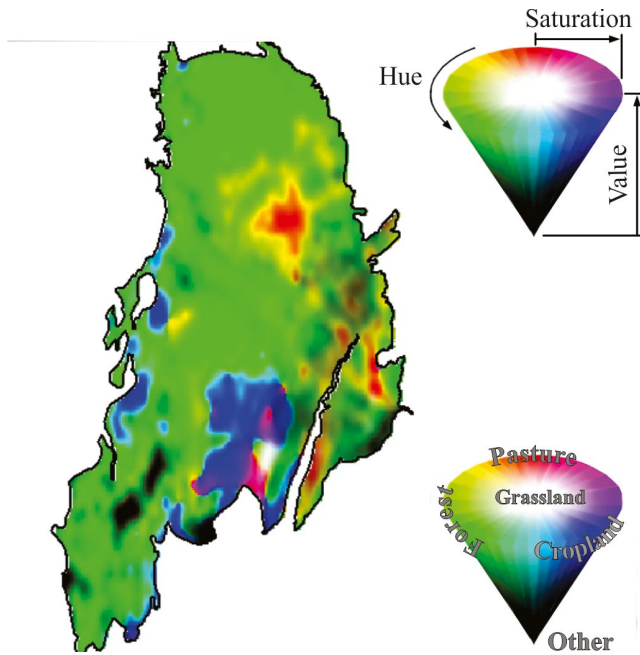


FIGURE 3 Synthetic LULC map. By using the HSV colour model, percentages of the five LULC classes are translated into a single colour. The sub-composition of Pasture-Forest-Cropland defines the hue, whereas $100 - \% \text{ Natural grassland}$ and $100 - \% \text{ Others}$ corresponds to saturation and value/brightness respectively. Thus, reddish areas are dominated by Pasture, bluish by Cropland, greenish by Forest, whitish by Natural grassland and blackish by Others

TABLE 2 Summary of the GDM (Generalized Dissimilarity Model) for the Gran Chaco. For each variable, the scores for the magnitude of effects (measured by summing the coefficients of the I-splines from GDM) are reported. The total explained deviance was obtained by subtracting the null deviance from the model deviance

Variables	Importance
Geographical distance (km)	0.25 (6.35%)
Annual precipitation	0.79 (20.05%)
Annual mean temperature	0.83 (21.07%)
% Pasture	0.04 (1.02%)
% Forest	0.18 (4.57%)
% Cropland	1.31 (33.25%)
% Natural grassland	0.02 (0.51%)
% Other	0.52 (13.2%)
Model deviance	595,716.28
Null deviance	119,897.43
Percent explained	79.87%

north-northwest-south-southeast, being the northern cluster more specious than the other. The divider between these two clusters coincides broadly with the Bermejo-Pilcomayo interfluvium and the Lower Paraná river. The interfluvium between the Bermejo and Pilcomayo rivers has been previously identified as a disjunction zone in bird distributions in southern South America (Nores, 1992; Short, 1975), where several pairs of species and subspecies show their

distributional limits. Many widespread Neotropical birds that enter the Gran Chaco from the north reach their southern distributional limits in this interfluvium (Nores, 1992; Short, 1975). Similarly, several species that enter the region from the south reach the northern limit of their distribution near this area. Also, tropical and subtropical climates (as determined by the Tropic of Capricorn) narrowly fit the distribution of the Northern and Southern clusters respectively.

Interestingly, the northern sub-region is supported by many species mainly associated with humid environments ranging from large water bodies to swamps and marshes in forests, in addition to forest species associated with wet forests (Table 1). Short (1975) had already stated that wetland-associated species were mainly distributed to the northeast of the region. Although most of these species are not exclusive from the northern sub-regions, their occurrence is higher there, owing to the greater availability of wetlands and wet forests. In turn, the northern sub-region is divided longitudinally into two well-defined areas, one to the west characterized mainly by forest birds, and one to the east long characterized by bird species that inhabit wetlands and flood grasslands (Table 1). There are no current geographical barriers that support this subdivision, but rather it reflects a climatic gradient of decreasing precipitation from east to west and the replacement of predominant habitat types from more humid to drier ones. Species supporting the southern sub-regions are mainly associated with mountainous and arid environments, including scrublands, xeromorphic forests and grasslands, all predominant environments in southern South America. These results reinforce the idea of the strong imprint of the climate on species distribution over which the effects of land use change described below are superimposed. Hence, the spatial correlate of our clustering result leads to a non-trivial discussion: splitting out of the Gran Chaco guided by its avifauna does not match the traditional bipartition into Dry and Wet Chaco sub-ecoregions. This last classification is largely based on the climatic gradient and floristic composition (Bucher, 1982; Olson et al., 2001), and divides the Gran Chaco longitudinally. The answer to the previous question is only partially affirmative because the northern sub-region includes all the Wet Chaco but also expands latitudinally to the north of Bermejo over the Dry Chaco.

Most species with restricted distributions within the Gran Chaco inhabit in the north and east, contributing to the greatest species richness in the northern communities. The occurrence of restricted-range species in this sub-region is presumably related to requirements of more humid conditions and the tropical distribution of most of these species (Short, 1975; Stotz et al., 1996). While an analysis of the biogeographic relationships between the Gran Chaco and the surrounding biomes is outside the objectives of this study, polarized colonization and latitudinal restriction to dispersal is probably the mechanism underlying the clustering configuration along the north-south axis. Examples are species that enter marginally in the region; they occupy very small areas in the Chaco and include species mostly distributed in neighbouring ecoregions like Amazonia, Chiquitano Forests and the Pantanal in the north (e.g. *Ramphocelus carbo*, *Nystalus chacuru*) or like

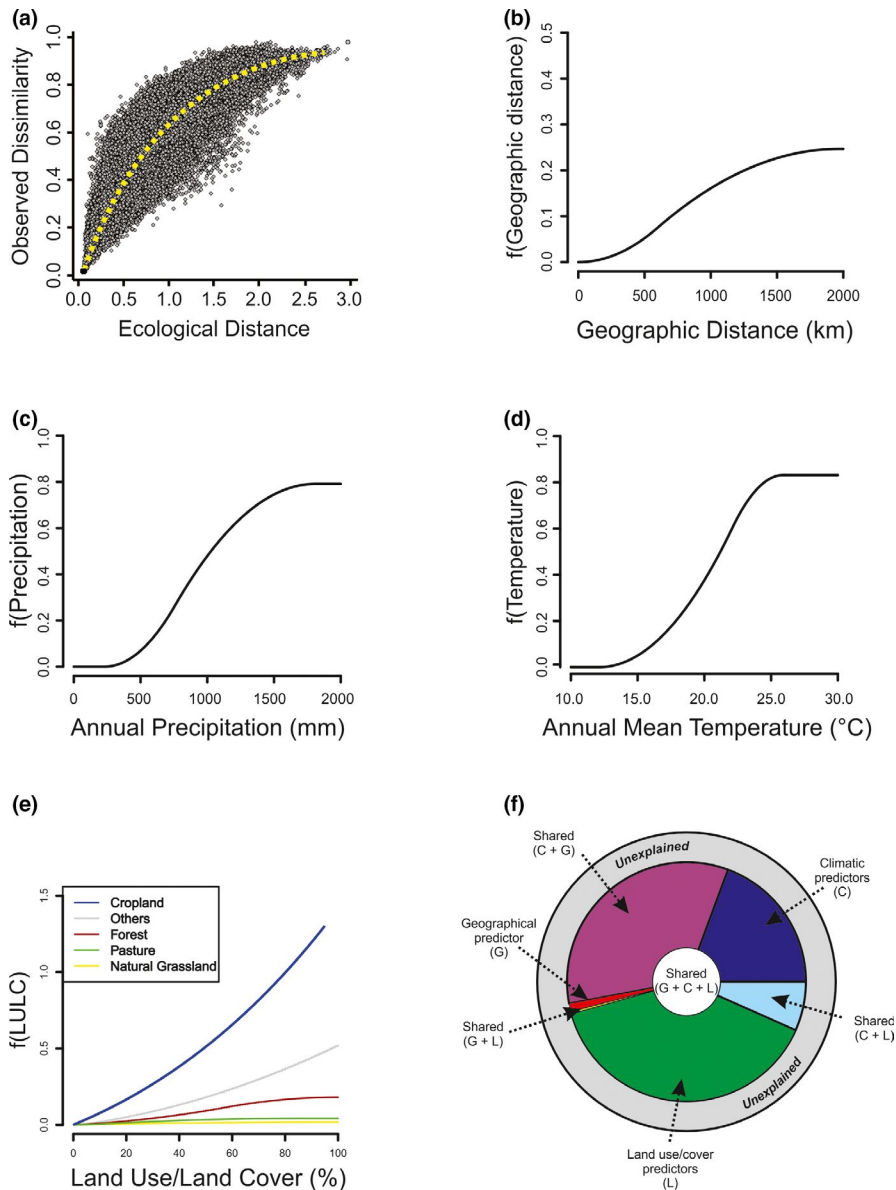


FIGURE 4 (a) Relationship between observed compositional dissimilarity and ecological distance between sites. The ecological distance between a pair of sites is calculated as the difference they have along the single linear predictor or gradient inferred (obtained by summation over differences across l-splines). (b–e) Generalized dissimilarity model represented by fitted l-splines (partial regression fits). Eight predictors were included in the model, and they deepen in geography, climate and LULC data. The maximum height reached by each curve indicates the total amount of compositional turnover associated with that variable (it also indicates the relative importance of that variable in explaining beta diversity), holding all other variables constant. The shape of each function indicates how the rate of compositional turnover varies along the gradient. (f) Partition of overall deviance of null model among unique and shared contributions of predictor classes

the sub-Andean mountain range and Patagonia in the south (e.g. *Sturnella loyca*, *Catamenia analis*).

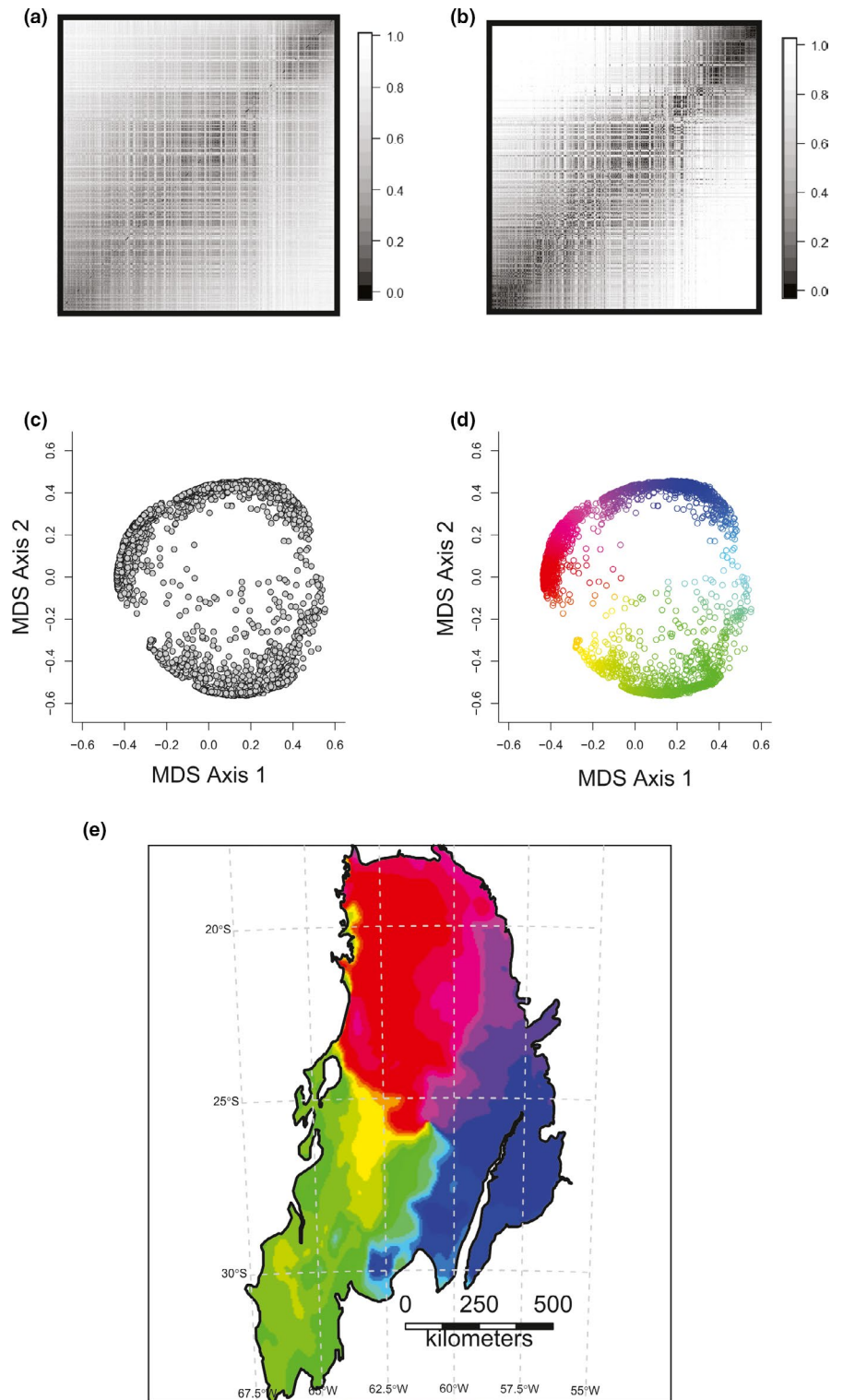
4.2 | Untangling the Gordian knot of β drivers

Remarkably, cropland was the single variable that more strongly influenced the beta diversity structure in the Gran Chaco. LULC tends to have stronger effects on biodiversity at small spatial scales (Jeliaskov et al., 2016), but in this study, we observed that they were strongly associated with beta diversity patterns at the regional scale. This highlights how human-driven landscape changes could be reshaping the beta diversity of birds within the region. The growing intensity of human impacts on ecosystems make transformed environments a pervasive feature of landscapes (Ellis, Klein Goldewijk, Siebert, Lightman, & Ramankutty, 2010). Where ecosystem-process modifications reached a given threshold, novel ecosystems with different properties

can emerge (Morse et al., 2014), resulting in unpredictable changes of alpha-, beta-, and gamma-diversity (Socolar et al., 2016). The growing areas devoted to croplands in the Gran Chaco may have already caused irreversible changes in the composition of bird communities.

Geographic distance was recorded as the main variable determining the beta diversity of different taxa, with climatic variables becoming more important on a coarser spatial scale (country scale), while land use showed a weaker effect but at a finer spatial scale (e.g. Keil et al., 2012). Jeliaskov et al. (2016) as well as Keil et al. (2012) reported the scale dependence between agriculture and biodiversity, where anthropization affected biodiversity at finer scales but not at the regional scale. Contrary to these results, we found that the unique contribution of geographic distance in explaining the beta diversity is not as large as expected. Although meaningful, the overall explanatory condition of a model including both geographic distance and climate is not considerably larger than that obtained with such variables acting alone since they both covary. Precipitation and

FIGURE 5 Quantitative procedure and final result during mapping of beta diversity. (a) Intensity matrix of dissimilarity matrix for the Gran Chaco (site-by-site matrix, $2,669 \times 2,669$, values between 0/pure black and 1/pure white). (b) Intensity plot of the reweighted dissimilarity matrix. Clusters are evident as dark blocks along the main diagonal. (c) Ordination diagram of data points derived from multidimensional scaling applied on the reweighted matrix. (d) Colour assignment using the hue wheel. (e) Bird beta diversity map for the South American Gran Chaco



temperature are spatially structured, with warmer and most rainy sites to the north and east respectively. Our results also contrast with the scale dependence of agriculture–biodiversity relationships. In the Gran Chaco, LULC was the main factor governing beta diversity patterns at the regional scale, highlighting the novelty of our study, as LULC was always considered a variable with local-scale effects.

Species habitat requirements are a key determinant of distributional shifts when human activities change the distribution of

habitats through land cover change (Baselga, Bonthoux, & Balent, 2015). Agricultural intensification decreases not only the alpha diversity of birds but also the beta diversity by landscape homogenization and structural simplification (Jeliakov et al., 2016; Karp et al., 2018). In dry forests, bird species richness can be diminished by habitat simplification, being lower in croplands than in forests (Macchi et al., 2013; MacGregor-Fors & Schondube, 2011; Mastrangelo & Gavin, 2014). In the Gran Chaco, two processes

could be shaping patterns of beta diversity through the conversion of natural areas to croplands. On the one side, a large proportion of land being converted to croplands (Baumann et al., 2016) can be shaping the beta diversity in the region through a homogenization process that reduces the alpha- and beta-diversity between croplands. On the other side, the conversion of natural habitats to agricultural systems allows the expansion of a different set of species to human-modified landscapes by moving through altered habitat matrices (Macchi et al., 2013; MacGregor-Fors & Schondube, 2011). As croplands are intercalated with forests that harbour a distinctive species composition, this process can promote an increase of beta diversity (Macchi et al., 2013). The combination of within-habitat homogenization and increasing between-habitat heterogeneity contributes to new patterns of beta diversity in transformed ecosystems, following a trajectory of beta diversity change under persistent anthropogenic pressure (Socolar et al., 2016).

Although our results provide a significant basis for new studies, it is important to highlight a number of cautionary statements. First, we used five LULC classes, which could be improved with more detailed and precise coverage variables that can better capture subtle differences in the use of the mosaic of habitats by bird species. Second, we used the same LULC variables for modelling individual species distribution and analysing beta diversity patterns. In spite of this, we do not expect circularity in data analyses, since the studies were focused on different entities (i.e. while habitat suitability models focus on the species level, GDM focuses on the community level). Third, the effect of croplands on bird beta diversity could mask the effect of forest cover, since the change in the percentage of cropland per site was highly inversely correlated with the change in forest cover (see Appendix S3). Lastly, as we were limited by the extension of the land use layers, we modelled the species distributions using occurrence data from the Gran Chaco region only. We acknowledge that more accurate patterns can emerge if species distributions are modelled using both occurrence data from their entire ranges and land use layers of a greater extent (e.g. covering all South America), high resolution and representing different dates, like those we employed. Unfortunately, land use layers of such characteristics do not yet exist.

In recent years, the Gran Chaco has been subjected to agricultural expansion and intensification (Baumann et al., 2017). It experienced one of the highest deforestation rates worldwide, mainly due to the expansion of soybean production and industrial cattle ranching (Baumann et al., 2017; Grau, Gasparri, & Aide, 2005). If this process continues without regulation, it could cause great and perhaps irreversible changes on the Chacoan avifauna (Semper-Pascual et al., 2018). For conservation purposes, it is essential to analyse not only the richness patterns but also compositional dissimilarities between sites (Devictor et al., 2010). The Chaco's protected area network is insufficient and sparse (Nori et al., 2016), so studies that explore in-depth the replacement and nestedness components of beta diversity make significant contributions (Baselga, 2010; Socolar et al., 2016). Detecting priority conservation areas is a huge challenge for conservationists and should be based on integrated views of alpha- and beta-diversity (Zwiener,

Lira-Noriega, Grady, Padial, & Vitule, 2018). In the Gran Chaco, the richest sites of the region are in the northeast, but analysing beta diversity patterns highlights the complementary importance of the southernmost sectors and the risks they face. This study is a substantial contribution to the knowledge of the South American Gran Chaco avifauna and how human activities are affecting it. Moreover, the non-anticipated strong effect of cropland coverage on the regional-scale diversity suggests a growing footprint of land use change over the geographical patterns of bird diversity in forest biomes. We hope that our results become a basis for future ecological studies and conservation decisions that take into account regional-level faunistic patterns, in order to protect the maximum possible diversity of this highly threatened ecosystem.

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DATA AVAILABILITY STATEMENT

The authors confirm that the data supporting the findings of this study are available within the article and its supplementary materials.

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BIOSKETCH

María Gabriela Návaro is a doctoral student at the Universidad Nacional de Tucumán. She is interested in bird ecology, and the main focus of her dissertation is the taxonomic, phylogenetic and functional beta diversity of birds of the South American Gran Chaco.

Author contributions: M.G.N., P.G.B. and R.T. conceived the study; M.G.N. and P.G.B. conducted the fieldwork and M.G.N. collected data from other sources and performed the habitat suitability models. M.G.N. and D.D.S. performed the analyses of both clustering and beta diversity modelling. M.B. accomplishes the geographical analysis of LULC. D.D.S. lucubrated and implemented the colour-based procedures of map drawing. All authors contributed to the interpretation of the results and writing of the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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APPENDIX 1

SOURCE OF SPECIES PRESENCE RECORDS

Data accessed by direct consultation of collections

Colección Ornitológica del Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' - MACN - Buenos Aires, Argentina

Data accessed through the VerNet (<http://vernet.org/>, accessed on March 2015)

American Museum of Natural History - AMNH - New York
Carnegie Museum of Natural History - CM - Pennsylvania, United States

Charles R. Conner Museum - CRCM - Washington, United States
Cornell University-Macaulay Library of Natural Sounds - CUML - New York, United States

Cornell University Museum of Vertebrates - CUMV - New York, United States



Delaware Museum of Natural History - DMNH - Delaware, United States

Florida Museum of Natural History - FLMNH - Florida, United States

Field Museum of Natural History - FMNH - Illinois, United States

University of Kansas Biodiversity Institute - KU - Kansas, United States

Natural History Museum of Los Angeles County - LACM - California, United States

Moore Laboratory of Zoology - MLZ - California, United States

Bell Museum of Natural History - MMNH - Minnesota, United States

Museum of Southwestern Biology - MSB - New Mexico, United States

Michigan State University MSU Michigan, United States

Museum of Vertebrate Zoology, UC Berkeley - MVZ - California, United States

North Carolina Museum of Natural Sciences - NCSM - North Carolina, United States

Sam Noble Oklahoma Museum of Natural History - OMNH - Oklahoma, United States

Queensland Museum - QM - Queensland, Australia

Royal Ontario Museum - ROM - Ontario, Canada

San Diego Natural History Museum - SDNHM - California, United States

South Australian Museum - SAMA - South Australia, Australia

Texas A&M University Biodiversity Research and Teaching Collections - TCWC - Texas, United States

Tall Timbers Research Station and Land Conservancy - TTRS - Florida, United States

University of Alaska Museum - UAM - Alaska, United States

University of Michigan Museum of Zoology - UMMZ - Michigan, United States

National Museum of Natural History, Smithsonian Institution - USNM - Washington, United States

University of Washington Burke Museum - UWBM - Washington, United States

Western Foundation of Vertebrate Zoology - WFVZ - California, United States

Yale Peabody Museum - YPM - Connecticut, United States

Other sources accessed via the Internet

Centro Geoespacial para la Biodiversidad de Bolivia del Museo de Historia Natural Noel Kempff Mercado (<http://www.museoelkempff.org/cgb/>).

Avian Knowledge Network, Cornell Lab of Ornithology - eBird, Bird Observation Checklist Database (<https://ebird.org/home>).

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